# Madoqua guentheri. By Steven C. Kingswood and Arlene T. Kumamoto

## *Madoqua* Ogilby, 1837

*Madoqua* Ogilby, 1837:137. Type species *Antilope saltiana* Desmarest, 1816.

*Rhynchotragus* Neumann, 1905:88. Type species *Madoqua guentheri* Thomas, 1894.

**CONTEXT AND CONTENT.** Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Superfamily Bovoidea, Family Bovidae, Subfamily Antilopinae, Tribe Neotragini, Genus *Madoqua*. A key to the species of *Madoqua* follows (adapted from: Ansell, 1971; Haltenorth and Diller, 1980; Lydekker and Blaine, 1914; Thomas, 1894; Yalden, 1978):

1 Lower m3 without third (posterior) lobe [except in some *M. saltiana swaynei* (Ansell, 1971)]; upper line of premaxillae slanting, not strongly curved; nasals longer; proboscis only moderately developed (subgenus *Madoqua*) .... 2
   Lower m3 with third lobe; upper line of premaxillae S-shaped, strongly curved; nasals shorter; proboscis more strongly developed (subgenus *Rhynchotragus*) ........ 3
2 Body mass ca. 2–2.5 kg; mean length of maxillary tooth row 29 mm .......................... *M. piacentinii*
   Body mass ca. 2.5–4 kg; mean length of maxillary tooth row 29.8–34.5 mm ...................... *M. saltiana*
3 Proboscis enlarged and elongated; premaxillae short, usually reaching only about halfway to nasals; nasals very short, forward extension equal to rear edge of p2, about 42 mm from end of premaxillae ...............*M. guentheri*
   Proboscis smaller and shorter; premaxillae longer, reaching nasals; nasals longer, forward extension equal to front edge of p1, about 33 mm from end of premaxillae *M. kirkii*

## *Madoqua guentheri* Thomas, 1894
### Guenther's Dik-Dik

*Madoqua guentheri* Thomas, 1894:324. Type locality "Central Ogaden, 3000 feet," Ethiopia, about 06°30′N, 42°30′E (Yalden et al., 1984:102).

*Madoqua [Rhynchotragus] nasoguttatus* Lönnberg, 1907:7. Type locality "20 kilometres S.W. of Lake Baringo, British East Africa" (=Kenya).

*Rhynchotragus hodsoni* Pocock, 1926:188. Type locality "Mt. Mega, Southern Abyssinia (=Ethiopia)," altitude 7,000 ft. 04°N, 38°E (Ansell, 1971:63).

**CONTEXT AND CONTENT.** Context as given above, Subgenus *Rhynchotragus* (Lydekker and Blaine, 1914). Meester et al. (1986) consider *Rhynchotragus* a valid subgenus, but its validity is questioned by Kingdon (1982). Four subspecies are listed by Ansell (1971) as follows:

*M. g. guentheri* Thomas, 1894:324, see above.

*M. g. hodsoni* Pocock, 1926:188, see above.

*M. g. smithii* Thomas, 1901:804. Type locality "About 30 miles S.E. of Lake Stephanie." Yalden et al. (1984:102) indicate the type locality is near the border of Ethiopia and Kenya (*nasoguttatus* Lönnberg is a synonym).

*M. g. wroughtoni* Drake-Brockman, 1909:51. Type locality "Foothills of Mt. Abul Kassim, Wabi River (=Webi Shebeli), Gallaland, Abyssinia (=Ethiopia), within 20 miles west of Sheikh Hussein. Altitude 3500 feet." 07°N, 40°E (Ansell, 1971:63).

*M. g. hodsoni* is based on a single specimen, a pale aberrant, whose skull is indistinguishable from *M. g. guentheri* (Drake-

Brockman, 1930). Geographically, however, *hodsoni* lies between *smithii* and *wroughtoni* (Ansell, 1971). The validity of *M. g. wroughtoni* also is questionable; origins of two specimens in the literature suggest an affinity with *M. g. guentheri* (Yalden et al., 1984). Drake-Brockman (1930) includes *nasoguttatus* in *M. kirkii*.

**DIAGNOSIS.** Dik-diks (*Madoqua*) are distinguished from other Neotragini by having a tuft of long hair on the crown and a pointed, elongated nose which is entirely covered with hair, except for the lower part of the nasal septum; the rhinarium is nearly absent (Bryden, 1899; Sclater, 1900). Dik-diks have the most mobile nose among antelopes, and in the subgenus *Rhynchotragus* (*M. guentheri* and *M. kirkii*), the nose is similar in appearance to that of a tapir (*Tapirus*) or saiga (*Saiga tatarica*; Poggesi et al., 1982). *M. guentheri* and *M. kirkii* are difficult to distinguish, and skins and skulls with intermediate or mixed characteristics are known (Ansell, 1971; East, 1988; Kingdon, 1982; Poggesi et al., 1982). They are similar in size and coloration, but *M. guentheri* is generally recognized by its longer, more flexible proboscis (Lydekker and Blaine, 1914; Fig. 1). Compared to *M. kirkii*, the skull of *M. guentheri* (Fig. 2) differs by having smaller teeth and shorter nasals and premaxillae; in *M. guentheri*, the nasal process of the premaxillae usually becomes thinner dorsally and falls short of touching the nasal, but the ventral portion of the premaxillae is longer and narrower (Poggesi et al., 1982; Thomas, 1894). Length of the nasal chamber exceeds the interorbital breadth in *M. guentheri*, but not in *M. kirkii* (Roosevelt and Heller, 1915). Means (and ranges) of length of nasals (in mm) of *M. guentheri* and *M. kirkii*, respectively, are: 13.1 (9.8–17.5, $n = 21$) and 19.7 (12.2–24.2, $n = 32$; De Beaux, 1923; Drake-Brockman, 1909; Hollister, 1924; Lönnberg, 1907; Thomas, 1894, 1901). Karyotypes of *M. guentheri* (2n = 48–50) and *M. kirkii* (2n = 46–48) are distinguishable by at least two, fixed, chromosomal rearrangements: a pericentric inversion and a tandem fusion (authors' unpublished data).

**GENERAL CHARACTERS.** Guenther's dik-diks are of small size and slender build (Fig. 1). The hindquarters are at the same level or slightly higher than the shoulder. Typical of Neotragini, coloration is cryptic with inconspicuous markings (Estes, 1991). Dorsal pelage is generally grizzled yellowish-gray, slightly fading to grayish-brown, light rust-red, or sandy on the flanks and legs and sandy-white on the chin, throat, breast, belly, and inside



FIG. 1. Adult male *Madoqua guentheri* (studbook number 121; see Kumamoto, 1995) at San Diego Zoo. Photograph by Ken Kelley.

FIG. 2. Dorsal, ventral, and lateral views of skull, and lateral view of mandible of an adult male *Madoqua guentheri* (British Museum of Natural History 30.1.2.45) from Lake Baringo, Kenya. Greatest length of skull is 116 mm, and biorbital width is 55 mm. Photographs by Peter Grubb.

thighs. The tail is short, haired dorsally, and naked ventrally. Guenther's dik-diks have a small head and long neck; portions of the face and ears are sandy, pale rufous, or grayish-red (Drake-Brockman, 1930; Haltenorth and Diller, 1980; Lönnberg, 1907). Males have short, black horns that are straight or curved slightly backward from the profile of the face and are curved slightly outward in the frontal view. The horns are elliptical at their base (transverse by sagittal diameter ca. 8.5 by 12 mm), but they become circular as they taper toward the tips; they are strongly ringed for about half of their basal portion (Drake-Brockman, 1930; Lönnberg, 1907). Eyes are large and placed anterolaterally; eyes, eyelids, and preorbital glands are black. Ears are large and white interiorly. The legs are relatively long and slender. Hooves are black, slender, and pointed anteriorly; the lateral hooves are minute (Roosevelt and Heller, 1915).

*Madoqua guentheri* is sexually dimorphic; females are larger and lack horns. In males, the long hairs of the crest cover two-thirds of the length of the horns; thus, it is somewhat difficult to distinguish males and females, even at a short distance (Drake-Brockman, 1930). The crest of males is longer, coarser, and usually brighter in color than that of females (St. Leger, 1935). Means (and ranges) of external measurements (in mm) of adult males and fe-

males, respectively, are: total length, 587.7 (500–680, $n = 11$), 635 (600–670, $n = 2$); length of tail, 31.6 (20–50, $n = 7$),—; length of hindfoot, 182.5 (165–205, $n = 6$), 203; length of ear, 71.6 (60–80, $n = 6$),—; length of horn, 82.3 (58–108, $n = 53$),—; basal circumference of horn, 36.8 (25–51, $n = 45$),—; distance between horn tips, 40.7 (25–64, $n = 46$),—; height at shoulder,—(324–355, $n = 9$),—(355–365, $n = 5$); height at sacrum,—(355–370, $n = 8$),—(370–390, $n = 5$); and body mass (kg), 3.72 (3.5–3.9, $n = 3$), 4.55 (4.5–4.6, $n = 2$; Beadles and Ingersol, 1968; Best and Raw, 1975; Bryden, 1899; De Beaux, 1923; Drake-Brockman, 1910; Hofmann, 1973; Lönnberg, 1907; Roche, 1979; Roosevelt and Heller, 1915; Sokolov et al., 1994; Thomas, 1901).

*Madoqua g. guentheri* is relatively small compared to *M. g. smithii*. Lydekker and Blaine (1914) suggested that the ears of the putative race *M. g. wroughtoni* are broader and larger than in other dik-diks, except *M. kirkii cavendishi*, to which it bears a superficial resemblance. Pelage coloration also varies geographically; however, certain hues (e.g., reddish and pinkish tints of ventral areas) are often a result of local soils; thus, they are of no taxonomic value (A. M. Simonetta, in litt.). The underparts of *M. g. guentheri* are pinkish buff (Lydekker and Blaine, 1914). In *M. g. smithii*, the middle of the body is washed with reddish-brown, the sides of the face, back of the ears, and lower legs are light buff, and the snout is bright tawny (Haltenorth and Diller, 1980; Roosevelt and Heller, 1915). Pelage of some specimens from Ethiopia tends to be lighter or darker than usual, as in *M. g. hodsoni* or *M. g. wroughtoni*, respectively (Haltenorth and Diller, 1980; Lydekker and Blaine, 1914; Pocock, 1926). The muzzle is spotted with white in *M. g. nasoguttatus*, hence the name *nasoguttatus*, but this characteristic also occurs in some specimens of *M. g. guentheri* and *M. piacentinii*, possibly due to small wounds inflicted by thornbushes (Lönnberg, 1907; St. Leger, 1935).

Dik-dik skulls have the following characteristics: in males, horn cores are situated behind the orbits; the orbits project conspicuously; premaxillae are very thin above P1, but they expand slightly toward their apices; premaxillae are level with the palate, but the basioccipital is slightly below that level; nasals are short and wide (width > length in *M. guentheri*); maxillae drop suddenly at the apex of the nasals; lachrymal fossae are large; tympanic bullae are somewhat inflated; and supraorbital foramina are small (Roberts, 1954; Roosevelt and Heller, 1915; Thomas, 1894). Compared to *M. g. guentheri*, skulls of *M. g. smithii* are larger and stouter, and skulls of *M. g. nasoguttatus* have shorter nasals (12 by 14 mm—Lydekker and Blaine, 1914; Thomas, 1901). Means (and ranges) of skull measurements (in mm) of *M. g. guentheri* ($n = 1–3$), *M. g. nasoguttatus* ($n = 1$); *M. g. smithii* ($n = 1–13$), and *M. g. wroughtoni* ($n = 1–6$), respectively, are: greatest length of skull, 108.4 (106.7–110),—, 114.2 (110–120), and 103.4 (100–111); condylobasal length of skull,—,—, 105.7 (100–112), and 95.2 (93–97); greatest breadth of skull, 52.2 (51.6–52.8), 59.5, 56 (53.0–59.3), and 53.6; breadth of braincase, 41.5, 42.5, 44.2, and—; length of maxillary toothrow, 33.7 (33.0–34.3), 37, 37.2 (33.4–39.7), and 31.8 (30.5–34.2); length of mandibular toothrow, 34.3,—, 38.8 (34.4–41.7), and 36.1; length of mandible,—,—, 81.6 (75.8–87.1), and 74.6 (De Beaux, 1923; Drake-Brockman, 1909; Elliot, 1897; Hollister, 1924; Lönnberg, 1907; Roche, 1979; Sclater and Thomas, 1896–1897; Thomas, 1894, 1901).

**DISTRIBUTION.** Guenther's dik-diks are endemic to the Somali Arid Zone of East Africa (Fig. 3). Their geographic distribution includes Somalia (except the central coastal strip and the extreme northeast and northwest), eastern and southern lowlands of Ethiopia, eastern and northern Kenya, northeastern Uganda, and extreme southeastern Sudan (Ansell, 1971; East, 1988; Kingdon, 1982; Yalden et al., 1984). *M. guentheri* is not known to occur within 30 km of the coast, being replaced there by *M. kirkii*, nor west of the Nile River (Drake-Brockman, 1930; Roosevelt and Heller, 1915); occurrence south of the Tana River is uncertain (East, 1988). In Somalia, *M. kirkii* is thought to be confined to the southern coastal region, south of the Shebelle River, with *M. guentheri* occurring farther north. The ranges of both species may overlap in the Juba-Shebelle drainage and along a narrow belt in Kenya from the interface of the Turkana basin and Kenya highlands to the Tana River drainage (Ansell, 1971; East, 1988; Kingdon, 1982; A. M. Simonetta, in litt.). Guenther's dik-diks are now absent from the northwestern corner of Somalia, and populations have been reduced in the Haud and lower Juba River drainage (East, 1988). Altitu-
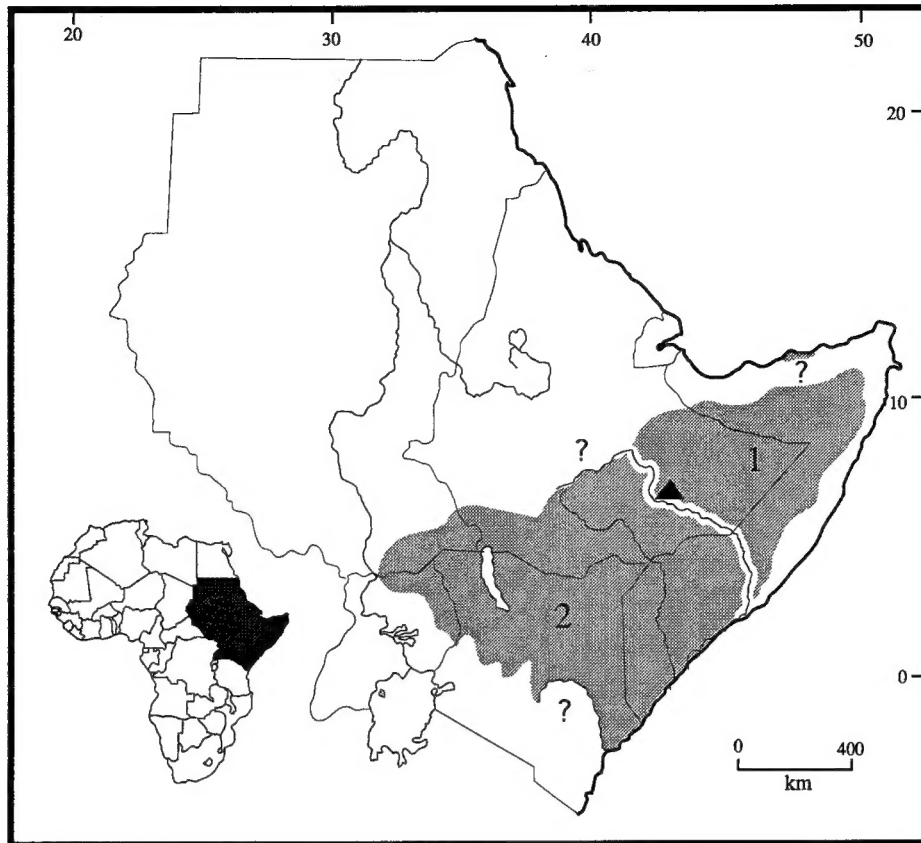
FIG. 3.  Distribution of *Madoqua guentheri* in East Africa and the type locality (triangle). Subspecies are: 1, *M. g. guentheri*; 2, *M. g. smithii*. A corridor along the Webi Shebeli River is unshaded to delineate the boundary between the two subspecies. Adapted from Ansell (1971), East (1988), Kingdon (1982), Roosevelt and Heller (1915), and Yalden et al. (1984). Map prepared by J. Jason Douglas.

dinally, *M. guentheri* is found from near sea level to about 2,100 m (Drake-Brockman, 1930; Pocock, 1926; Yalden et al., 1984).

**FOSSIL RECORD.** Fossil *Madoqua* appeared during late Miocene southwest of Lake Turkana, and *M. avifluminis* (formerly referred to *Praemadoqua*) has been found in Pliocene fauna of Tanzania. Dentitions and horn cores from both strata have an affinity to the subgenus *Rhynchotragus* (Gentry, 1978; Savage and Russell, 1983). Compared to living dik-diks, the molars of *M. avifluminis* show more traces of basal pillars, and the horns are shorter and thicker (Gentry, 1978, 1990).

**FORM AND FUNCTION.** Pelage is thin on the withers, and hairs are arranged in irregular rows. Hair is of one type with four size groups; in males, mean lengths are 13.2, 18.6, 23.0, and 27.2 mm. Hair length is 2–3 mm shorter in females, and their pelage is thinner; hair density is $1429/cm^2$ (Sokolov et al., 1994). Cross-sections of the hair shaft are oval at its base; higher on the shaft, they are bean-shaped. Cuticle scales of the shaft are square-shaped, producing a cuticular pattern that differs from that of *M. saltiana*. There are vibrissae on the lips (Sokolov et al., 1994).

The skin of *M. guentheri* is of median thickness among 16 species of Ethiopian ungulates and is thicker dorsally than ventrally. Subcutaneous fat tissue is poorly developed, but males have fat deposits between the digits and on the breast and withers (Sokolov et al., 1994). Guenther's dik-diks have four inguinal mammae (Roosevelt and Heller, 1915). Other skin glands include preorbital, palpebral, pedal, Meibomian, labial, nasolabial, anal, and vulval glands; these are composed of sebaceous and apocrine glands, except the Meibomian and nasolabial glands, which lack apocrine components (Pocock, 1910; Sokolov et al., 1994). Preorbital and pedal glands are also composed of sudoriferous glands and are used for scent marking. Preorbital glands consist of a white layer of apocrine sudoriferous tubules surrounding a black core of sebaceous glands; the apocrine glands produce a clear secretion, and the sebaceous glands secrete exudates containing melanin or lip-

oids, all of which combine in a central duct to form a black, tarry substance that is nearly odorless to humans (Estes, 1991; Gosling, 1985; Ono et al., 1988; Richter, 1971; Walther, 1984). Compared to other antelopes, Guenther's dik-diks have large (ca. 17 by 16 by 8 mm) preorbital glands in relation to their body size (Fig. 1); males have larger preorbital glands than females (Sokolov et al., 1994; Spinage, 1986). Pedal glands consist of a deep invagination (ca. 9 by 4 mm) that opens ventrally between the two digits on each foot (Gosling, 1985; Sokolov et al., 1994). Ultrastructural characteristics of the parotid gland of Guenther's dik-diks are consistent with 10 other species of East African ungulates, including grazers, other concentrate selectors, and intermediate feeders (Kayanja and Scholz, 1974). Salivary gland fragments are present in the lips (Sokolov et al., 1994). The density of sweat glands in dik-diks is $190/cm^2$, similar to that found in dromedaries (*Camelus dromedarius*), goats (*Capra hircus*), and sheep (*Ovis aries*), but much less than the $1,500/cm^2$ in cattle (*Bos taurus*; Maloiy, 1973; Wilson, 1989). Sweat glands of dik-diks and other bovids appear to be under adrenergic-neuron control (Maloiy, 1973).

Guenther's dik-diks have long hindlegs with the metatarsals nearly as long as the forelimbs; lumbosacral height is greater than shoulder height. In a standing position, their back is rounded, and the hindlegs are kept flexed with the femur and tibia folded toward the body. This posture is typical when they walk through dense bush vegetation, possibly an adaptation to quick starts and turns and long leaps (Estes, 1991; Hofmann, 1973). Forty-six measurements of the limb bones of *M. guentheri* are recorded by Scott (1985). Among 108 species of Bovidae, including *M. guentheri*, lengths of radius, metacarpal, and metatarsal do not scale predictably with body weight, suggesting that body size is less important in determining lengths of these bones than is adaptation to a particular habitat (Scott, 1985). Hooves are >15 mm long (Lönnberg, 1907). The skeleton of *M. guentheri* is illustrated by Hofmann (1973). The skull resembles that of other mammals having a trunk-like snout (e.g., saiga); nasals are reduced in size, and the nasal

chamber is enlarged to accommodate the proboscis (Bryden, 1899; Poggesi et al., 1982; Roosevelt and Heller, 1915). Compared to the neurocranium, the visceral portion of the skull is small, possibly due to retention of juvenile or fetal features (i.e., limited allometric development of the facial skull), or it may be considered a primitive trait along with the dik-dik's small size (Poggesi et al., 1982). Lachrymal pits are large and shallow to accommodate the preorbital glands. Short nasal bones, large lachrymal pits, and the large narial opening of the dik-dik skull allies *Madoqua* closer to *Gazella* than to other Neotragini (Roosevelt and Heller, 1915). However, the skulls of dik-diks and gazelles may be similar as a result of similar adaptations for arid environments (Estes, 1991). The modified ethmoid turbinal may function as a whistle (Kingdon, 1982). Male dik-diks have simple horn cores which are short, small, and straight (Gentry, 1978). Although females lack horns, small horn cores on the upper surface of the frontals occur on the skulls of a few females (Poggesi et al., 1982). The dental formula is: i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Haltenorth and Diller, 1980). In *M. guentheri* and other selective, Neotragini browsers, medial lobes of the upper molars and labial lobes of the lower molars are sharply angled (Gentry, 1990).

Head musculature of *M. guentheri* is described by Saber (1987). Among 22 species of ruminants, including *M. guentheri*, mass of the bilateral masseter muscle is significantly correlated with body mass regardless of body size and feeding type, amounting to ca. 0.20% of body mass in all species (Axmacher and Hofmann, 1988). Arrector pili are relatively large (Sokolov et al., 1994).

Blood (n = 2–74) of *M. guentheri* is characterized by: 2,153 white blood cells/mm³ (range, 800–4,800); 11.48 million red blood cells/mm³ (range, 6.0–19.9); hemoglobin of 15.7 g/100 cm³ (range, 7.9–19.9); hematocrit of 47.6% packed-cell volume (range, 26.0–68.0); mean corpuscular volume of 42.2 μm³ (range, 21.9–77.3); mean corpuscular hemoglobin content of 13.7 pg (range, 8.1–26.5); mean corpuscular hemoglobin concentration of 32.8 g/100 cm³ (range, 24.3–40.7); 857 neutrophilic granulocytes/mm³ (range, 42–2,850); 1,212 lymphocytes/mm³ (range, 216–2,460); 156 monocytes/mm³ (range, 16–576); 33 eosinophilic granulocytes/mm³ (range, 16–56); 263 basophilic granulocytes/mm³ (range, 20–1,025); and 15 band-type neutrophilic granulocytes/mm³ (range, 14–15). Means (and ranges) of blood chemistry values (n = 2–9; in mg/100 ml) are: calcium, 9.0 (0.8–11.5); phosphorus, 10.0 (3.3–17.7); blood urea nitrogen, 23 (13–34); creatinine, 1.1 (0.6–1.4); uric acid, 0.6 (0–1.2); glucose, 133 (11–217); cholesterol, 84 (39–145); total bilirubin, 0.7 (0.2–1.3); direct bilirubin, 0.1 (0–0.4); and indirect bilirubin, 0.4 (0.1–0.9; International Species Information System, 1995). The spleen is relatively small; volume is 60–135 ml and size averages 65 by 45 mm (Hofmann, 1973; Lönnberg, 1912).

Per kg body weight, Guenther's dik-diks consume about twice as much dry matter and produce three times the amount of food energy as cattle, but compared to grazers, they are inefficient in breaking down cellulose (Hofmann, 1989; Hoppe, 1977). Guenther's dik-diks are concentrate selectors, feeding selectively on dicotyledonous plants that can be rapidly fermented, ruminated, and passed through the stomach, i.e., plants that are rich in protein, fat, and moisture but are relatively poor in fiber and cellulose (Hofmann, 1973; Hofmann and Stewart, 1972). Plant selection may be based on olfactory cues. Guenther's dik-diks have a relatively large mouth, which allows the sideways stripping of branches or the gnawing of flowers and fruit (Hofmann, 1989). Concentrate selectors such as *M. guentheri* have a relatively small stomach capacity and weight, ca. 8–10% of body weight when full and ca. 2% when empty, compared to 14–15% when full and 3–3.5% when empty in roughage grazers. The gastrointestinal tract of *M. guentheri* is illustrated by Hofmann (1973) and Stevens (1988). Averages (and ranges) of capacity (in ml) of the rumen and reticulum and the omasum and abomasum are 750 (560–1,050) and 100 (60–135), respectively; the sequence of sizes of the stomach compartments is: rumen, reticulum, abomasum, and omasum (Hofmann, 1973). Stomach contents from dik-diks weigh ca. 300–500 g (Kingdon, 1982). The rumen is a simple, folded tube with dense papillation that increases the absorptive mucosal surface by 15 to 17 fold; rumen pillars, which function as food retaining barriers, are poorly developed. The muscular omasum has little surface enlargement, but it has a horny papillation that suggests a grinding and straining function. Specialization for the diet also involves the rumen blindsacs and omasal mucosae (Hofmann, 1973; Hofmann and Stewart, 1972;

Lönnberg, 1912). There is little ultrastructural variation in the abomasal epithelium of 10 species of roughage grazers, intermediate feeders, and concentrate selectors, including *M. guentheri*; however, there are greater differences with respect to morphology of the glandular tubules and arrangement of the epithelial cell types (Weyrauch and Saber, 1985). Guenther's dik-diks ruminate throughout the day, especially during active feeding periods; 5–15 min periods of rumination alternate with equal periods of feeding. Relatively large salivary glands supply buffered liquid in sufficient quantity to maintain constant rumenal pH (Hofmann, 1973). Approximate lengths of the small and large intestines are 360 cm and 159 cm, respectively. Left and right lobes of the liver measure 76 by 45 mm and 78 by 66 mm, respectively; the Spigelian lobe is rounded, but not prominent, and the gall bladder is very small (Lönnberg, 1912).

Minimum water requirements (in l/100 kg body weight/day) of dik-diks, including *M. guentheri*, range from 5.59 (at 22°C) to 7.72 (at 22°C for 12 h, then 40°C for 12 h). Although having a larger surface/volume ratio and higher water requirements than larger species, dik-diks probably do not drink for much of the year, unless fed dry foods in captivity (Kingdon, 1982; Maloiy, 1973). Rapid passage of large amounts of food through the digestive tract increases the ingestion and retention of plant-borne water (Hoppe, 1977). Methods of conserving water and avoiding heat stress that are used by dik-diks include: licking condensation droplets that form on the nose; reabsorbing water from feces; concentrating and restricting urine output; limiting cutaneous evaporation; storing body heat; lowering metabolic rate; thermal panting; and reducing midday activity (Estes, 1991; Hoppe, 1977; Kingdon, 1982; Maloiy et al., 1988; Schoen, 1972). Dik-diks can save 3.5–5.0 ml H₂O/kg body mass/day through the process of heat storage; under heat stress, body temperature can increase as much as 4.1°C above the normal average of 37.8°C (Maloiy, 1973; Schoen, 1972). Captive Guenther's dik-diks are able to avoid urination for 24 h (Fitzgerald and Hnida, 1994a). Among nine species of desert ungulates examined, they have the highest urine concentration (up to 4,762 mosmol/kg H₂O) and the lowest water content in feces (55–98 g H₂O/100 g dry feces); among mammals that have been studied, dik-dik kidneys rank second to those of kangaroo rats (*Dipodomys spectabilis*) and desert jerboas (*Jaculus jaculus*) in urine concentrating ability (Maloiy, 1973; Maloiy et al., 1988; Schoen, 1969, 1972). This ability is probably due to the kidney's relatively high volume (47%) of renal medullae and its long loops of Henle (Schoen, 1969).

In terms of evaporative cooling, dik-diks seem to conform to the small antelope model of panting preferentially over sweating; the respiratory tract seems to be the primary avenue for dissipating excess heat during periods of thermal stress (Maloiy, 1973; Maloiy et al., 1988; Wilson, 1989). When under heat stress, dik-diks have a fast, shallow panting rate, which reaches nearly 400 cycles/min, or about 12 times the normal rate (Schoen, 1972). The most obvious adaptation for avoiding heat stress is modification of the nose to allow cooling the blood by nasal panting (Estes, 1991; Kingdon, 1982). The proboscis enlarges the nasal vestibule and the mucosal area available for evaporative cooling; the flexible trunk functions like a bellows to increase air flow, and the tiny nostrils and hairy muffle help to minimize water loss (Hoppe, 1977). Cooled blood drains from the nasal linings to surround the carotid rete in the cavernous sinus. Blood cooled in the carotid rete is then carried to the brain for further heat exchange; thus, blood going to the brain is cooled first, where the danger of overheating is most detrimental. Overheated animals also may compensate by resting in the shade, orienting their body surface to maximize convective cooling, and spreading saliva over their flanks (Hoppe, 1977; Kingdon, 1982; Schoen, 1972).

The ovary of Guenther's dik-dik is similar in structure to that of other ruminants, particularly Kirk's dik-dik. Mean size of the ovaries (n = 14) is 6.5 by 3.6 mm (Kayanja and Sale, 1975; Lönnberg, 1912). When ca. 20 μm in diameter, oocytes associate with attenuated epithelial cells to form the primary follicles. Follicles probably grow to ca. 1 mm in diameter before the onset of ovulation; throughout pregnancy, the largest follicles measure ca. 4.6 mm in diameter. Only one follicle ruptures during each estrous cycle. The zona pellucida is well developed when diameters of the oocyte and follicle, respectively, reach 40 μm and 80 μm. Follicular atresia affects follicles of all sizes, especially larger follicles with diameters of up to 3 mm; follicles with more than one oocyte and oocytes with more than one nucleus occur occasionally. The corpus luteum

is solid and measures 3–7 mm in diameter (Kayanja and Sale, 1975; Maloiy et al., 1988).

**ONTOGENY AND REPRODUCTION.** Guenther's dik-diks reach sexual maturity before 1 year of age. In captivity, a few precocious females conceive at less than 4 months of age, and males can sire offspring before 5 months of age. Guenther's dik-diks can remain reproductively mature past 10 years of age; a calf was sired by a male at about 10 years, 5.5 months, and a female gave birth at an estimated 13 years (Kumamoto, 1995). Mean duration and range (in days), respectively, of estrus ($n = 12$, $n = 160$) are 1.48 ($SE = 0.86$) and 1–7, during which females exhibit lordosis (standing with a decurved flexing of the spine). Estrus is also indicated by low levels of immunoreactive pregnanediol-3-glucuronide (iPdG), a urinary progesterone metabolite; low levels occur either immediately prior to, during, or immediately following estrus (Fitzgerald and Hnida, 1994b). Soil-extracted urine can be used to monitor iPdG levels (Hnida and Fitzgerald, 1992). Mean interval and range (in days), respectively, between estrus ($n = 10$, $n = 94$) are 17.54 ($SE = 1.45$) and 13–21 (Fitzgerald and Hnida, 1994b).

Implantation is unilateral, usually occurring in the right uterine horn but rarely in the left (Kayanja and Sale, 1975; Lönnberg, 1912). Gestation periods of 170–180 days have been reported (Fitzgerald and Hnida, 1994b). Guenther's dik-diks give birth to one calf, but there is an unconfirmed report of twins (referred to as "*kirkii*"—see REMARKS). In Ethiopia, births occur during August and September; in captivity, parturition occurs throughout the year, but peaks during April–June and November–January (Kumamoto, 1995; Kurt, 1964). Of 126 captive births of known sex, 60 were females and 66 were males (Kumamoto, 1995). In dik-diks, postpartum estrus occurs about 10 days after birth, such that for a given female, mating and parturition can take place twice yearly at about the same time. Thus, females are pregnant for most of the year, even when accompanied by dependent young (Estes, 1991; Kingdon, 1982; Ono et al., 1988; Spinage, 1986). In captivity, the interbirth interval averages 193 days and ranges from 169 to 289 ($n = 71$; Kumamoto, 1995).

Birth, care, and development of neotragine offspring are apparently typical of hider species; neonates are precocious, but they do not accompany their mother immediately (Estes, 1991). Dik-dik calves remain concealed for their first 2–3 weeks, and apparently during this time, mothers approach to about 10 m from their infant and wait for it to appear before making contact (Haltenorth and Diller, 1980; Spinage, 1986). In captivity, mothers may approach to within a few meters, or closer, to initiate nursing (J. A. Hnida, in litt.). To facilitate concealing the calf, female dik-diks eat the afterbirth. After the hiding period, young begin to follow their mother and will accompany both parents for a few months (East, 1988; Haltenorth and Diller, 1980). Females nurse their young for up to 3–4 months, but calves begin to eat solid food after 1 week (Estes, 1991; Haltenorth and Diller, 1980). A satisfactory diet for hand-raising dik-diks was cows' milk composed of 3.4% protein, 3.6% fat, 4.7% sugar, 12.3% total solids, and 65 calories/100 gm. On this diet, calves were initially bottle-fed five to six times/day; feedings were gradually reduced after 6 weeks, and weaning occurred at 7–9 weeks (Hutchison, 1970b).

A Guenther's dik-dik fetus is described by Ghidini (1939). Fetuses range in length (crown–rump) from 3 to 5 cm ($n = 2$; Kayanja and Sale, 1975). In captivity, mean mass (in g) of calves at birth is 684 ± 100 ($n = 10$); female calves average 697 ± 91 ($n = 6$) and male calves average 664 ± 123 ($n = 4$). After 21 days of growth, mean mass (in g) of calves is 1,435 ± 165 ($n = 10$); female calves average 1,452 ± 108 ($n = 6$) and male calves average 1,403 ± 277 ($n = 4$; Luce, 1989). Although females are significantly heavier than males, both at birth and after 21 days of growth, relative weight gain/day is the same for both sexes (4.8%); during the 21-day period, growth rates of females and males, respectively, are 108% and 111% (Luce, 1989). Body masses (in kg) and age (in parentheses) of Guenther's dik-dik calves are: 1 (2–2.5 weeks), 2 (8.5–12 weeks), 2.8 (118 days), 3 (28 weeks), and 2.5 (1 year; Frazier and Hunt, 1994; Hutchison, 1970a; Schoen, 1972). Mean masses (and ranges, in kg) of adolescent females ($n = 2$) and males ($n = 5$), respectively, are 4.45 (3.9–5.0) and 3.76 (3.3–4.5; Ono et al., 1988). Dik-diks reach adult height by the age of 8 months and adult mass at 12–18 months (Estes, 1991; Haltenorth

and Diller, 1980; Hofmann, 1973; Hutchison, 1970a; Kingdon, 1982).

The color pattern of Guenther's dik-diks at birth is identical to that of adults, and the ears, nose, and legs are generally well-developed at birth (Hutchison, 1970a; Roosevelt and Heller, 1915). In captivity, calves have difficulty standing on smooth floors until they learn to walk on the tips of their hooves; thus, mats are used to prevent slipping (Hutchison, 1970b). Horns emerge at 7–9 weeks but are initially concealed by the crest; they reach full size at 2 years (Estes, 1991; Hutchison, 1970a). Horn annulations begin to appear at 34 weeks of age. At a few days of age, only incisors and canines are erupted (Hutchison, 1970a). Skulls in which the first molars are erupting have well-developed upper canines, which are absorbed by the time the second molars are erupted. Similar canines are found in *Gazella* at the same age, but they have not been observed in other genera of antelopes (Roosevelt and Heller, 1915). In newly born *M. guentheri*, premaxillae reach nasals and are as long as in *M. kirkii*; however, the nasal process of the premaxillae is very thin, and it breaks after birth. The broken upper third of the premaxillae then fuses with the maxillae, such that premaxillae in adult skulls do not appear to reach nasals (Poggesi et al., 1982). Longevity in the wild averages 3–4 years but may reach 7–8 (Haltenorth and Diller, 1980; Hofmann, 1973). A captive-born male was still alive at the age of 11 years, 9 months, and a wild-caught female, estimated to be 4 years of age at the time of capture, was still alive after 10 years, 1 month in captivity (Kumamoto, 1995).

**ECOLOGY.** Guenther's dik-diks are never far from cover, and all of their habitats are typified by low, thicket vegetation, such as arid and semiarid thornbush, savanna grassland-woodland, and riverine grassland-woodland. They are common in disturbed or over-grazed areas; regenerating bush, old fields, and roadsides are especially favored, possibly because disturbed habitats have abundant food at a level they can reach (East, 1988; Kingdon, 1982; Kurt, 1964). Habitats range from areas with alluvial hardpans and sandy soils to lava gravel flats and low, rocky hills (Coe, 1972; Drake-Brockman, 1930; Kingdon, 1982; Sclater and Thomas, 1896–1897). As a percentage of the total area occupied by individual animals, means (and ranges) of habitat types occupied by Guenther's dik-diks ($n = 1$–5) in Omo National Park, Ethiopia are: *Combretum-Sehima* bush ($n = 5$), 56.1 (46.6–65.4); *Acacia mellifera* savanna ($n = 2$), 33.1 (24.4–41.8); riverine forest ($n = 3$), 11.6 (2.0–23.5); human settlements ($n = 5$), 10.0 (5.2–22.1); old field ($n = 3$), 9.0 (1.5–16.1); *Ischaenum-Pennisetum* grassland ($n = 3$), 8.2 (3.7–13.3); *Combretum* forest ($n = 1$), 3.4; *Acalypha-Sanseviera* thicket ($n = 5$), 2.6 (1.3–3.3); *Acacia nilotica* savanna ($n = 1$), 0.7 (Ono et al., 1988). Other dominant vegetation of Guenther's dik-dik habitats includes *Aloe, Colophospermum, Commiphora, Dobrera, Juniperus, Opuntia,* and *Salvadora* (Coe, 1972; Drake-Brockman, 1930; East, 1988; Estes, 1991; Kingdon, 1982; Kurt, 1964; Roosevelt and Heller, 1915). Electivity indices for Guenther's dik-diks ($n = 5$) in open and closed habitats, respectively, are −0.72 to +0.08 and −0.03 to +0.14 (Ono et al., 1988).

Like most neotragines, Guenther's dik-diks eat leaves and flowers of forbs and leaves, stems, flowers, fruits, seeds, and pods of shrubs and trees, frequently in the form of litter, and some bulbs. Occasionally, they nibble at the tips of new grass, but grasses make up little of their diet, except for flowers and seeds (Estes, 1991; Hofmann and Stewart, 1972). Dik-diks may select one leaf only to drop it in favor of another. As concentrate selectors adapted to dry conditions, Guenther's dik-diks take the place of tiny forest neotragines in the transition from moist to dry savanna woodland because they can utilize abundant and protein-rich shrubs and trees and many xerophytic succulents (Spinage, 1986). Guenther's dik-diks eat acacias (Leguminosae: *Acacia*), combretums (Combretaceae: *Combretum*), spiderworts (Commelinaceae: *Commelina*), spurges (Euphorbiaceae), stonecrops (Crassulaceae: *Kalanchoe*), buckthorns (Rhamnaceae), salvadoras (Salvadoraceae), grasses (Gramineae: *Sehima*), and nightshades and clearing nuts (Solanaceae: *Solanum, Strychnos*; Hofmann, 1973; Ono et al., 1988; Roosevelt and Heller, 1915). Dik-diks also browse on crops and orchards (Estes, 1991; Kurt, 1964). In captivity, Guenther's dik-diks are fed alfalfa, pelleted grain, fruits, vegetables, fresh browse, and they are provided with a mineral/salt block (Anonymous, 1957; Bunn, 1988; Hnida et al., 1992; Hutchison, 1970b). Dik-diks obtain water from plant juices and dew, and apparently they can survive without sur-

face water; a Somali legend holds that a dik-dik will die if it drinks (Drake-Brockman, 1930; Hofmann, 1973; Roosevelt and Heller, 1915).

According to Roosevelt and Heller (1915), dik-diks are rarely seen in densely vegetated habitats because of their alert and timid nature, but Sclater and Thomas (1896–1897:91) state "sometimes the undergrowth seems to be alive with them." Population densities of Guenther's dik-diks (in animals/km²) were 0.01–0.03 in northeastern Uganda, 0.3–10.1 in eastern Ethiopia, 23.8 in Omo National Park, Ethiopia, and 64 in South Turkana, Kenya; estimated biomass of the South Turkana population is 263 kg/km² (Coe, 1972; Eltringham and East, 1989; Kurt, 1964; Ono et al., 1988). In Raume Erer, Ethiopia, densities (in animals/km²) were higher in gallery forest than savanna, 3.8–10.1 versus 2.2–3.0; densities were higher during the rainy season in both habitat types. This population ranged from 52% to 78% female and 22% to 48% male (Kurt, 1964).

*Madoqua guentheri* is sympatric with *M. kirkii* in Kenya and possibly Somalia, and is sympatric with *M. saltiana* in Ethiopia and Somalia. *M. guentheri* replaces *M. saltiana* in the arid savanna of southern Ethiopia. In Somalia, they are ecologically separated as *saltiana* is found in more open habitats with few, if any, tall bushes and trees (Ansell, 1971; Kingdon, 1982; A. M. Simonetta, in litt.; Yalden et al., 1984). Dik-diks benefit from the feeding activities of larger herbivores; elephants (*Loxodonta africana*) fell trees and break branches, giraffes (*Giraffa camelopardalis*) drop branches, and larger antelopes keep food plants browsed to within reach of dik-diks (Estes, 1991). Klipspringers (*Oreotragus oreotragus*) are possible competitors for food during the dry season (Kingdon, 1982).

Predators of dik-diks include silver-backed jackals (*Canis mesomelas*), spotted hyenas (*Crocuta crocuta*), wild cats (*Felis silvestris*), caracals (*Caracal caracal*), servals (*Leptailurus serval*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), Verreaux's eagles (*Aquila verreauxii*), martial eagles (*Polemaetus bellicosus*), rock monitors (*Varanus exanthematicus*), and rock pythons (*Python sebae*; Brown and Amadon, 1968; Haltenorth and Diller, 1980; Jones et al., 1988; Kingdon, 1982). Guenther's dik-diks are hosts of the louse *Damalinia victoriae*, tick *Amblyomma variegatum*, cestode *Taenia madoquae*, and nematode *Impalaia tuberculata*, which is a widespread cause of intestinal parasitosis in dromedaries (Hopkins and Clay, 1952; Jones et al., 1988; Morel and Rodhain, 1972; Sobrero and Mussa, 1975). Only the larval stage of *T. madoquae* is found in dik-diks, in their muscle tissue; the adult tapeworm is found in the gut of silver-backed jackals, illustrating the predator-prey relationship between dik-diks and jackals (Jones et al., 1988). Rumen protozoa are either absent or represented only by *Entodinium* sp., possibly because of a lack of cellulose in the dik-dik's diet (Wilson, 1989).

Guenther's dik-diks are common throughout much of their range in Kenya and Sudan, widespread in southern and eastern Ethiopia and between the Shebelle and Juba Rivers in Somalia, and locally common, but widespread, in northeastern Uganda (East, 1988). In Somalia and Uganda, their scrub and thicket habitats have probably benefited by ecological changes that resulted from overgrazing by domestic livestock and by an increase in fallow and disturbed vegetation that accompanied the spread of human settlement. Although severe habitat degradation and overhunting have greatly reduced antelope populations in regions of Somalia (e.g., the central coast, Haud, and lower Juba River drainage), Guenther's dik-diks have survived, but their numbers have decreased in closely settled areas due to hunting (East, 1988). *M. guentheri* populations are estimated to number over 100,000 and are not considered threatened; however, they could be at risk in coming years because there are fewer than three populations of at least 5,000 animals each that are in well-protected and managed areas (East, 1988, 1992). Parks and reserves with populations of Guenther's dik-diks exist in Ethiopia (Chew Bahar, Harrar, Mago, Nechisar, Omo, Tama, and Yavello), Kenya (Arawale, Boni-Dodori, Lake Bogoria, Losai, Marsabit, Meru, Rahole, Samburu-Isiolo, Shaba, Sibiloi, and possibly Tsavo), Sudan (Boma and Kidepo), and Uganda (Bokora, Kadam-Debasien, Kidepo Valley, and Matheniko). Somalia does not have a system of conservation areas, but several localities have been proposed for protection; those with populations of Guenther's dik-diks include Arbowerow, Daalo Forest, Far Wamo, Hargan-Dalandoole, Lake Dere, and Las Anod-Taleh-El Chebet

(East, 1988). The captive population in North America numbers 79 (Kumamoto, 1995).

During the early 1900s, hundreds of thousands of dik-dik skins were sold by Hawiya Somalis each year in Mogadishu for export (Drake-Brockman, 1911, 1930). Guenther's dik-diks are still frequently hunted, legally and illegally, throughout their range. Legal take is limited or restricted in Ethiopia, where four males may be taken on a general hunting license, and in Sudan, where they may be hunted outside protected areas but only with traditional methods (East, 1988). Traditionally, they have been hunted with bows and arrows, dogs, nets, and traps (Drake-Brockman, 1911; East, 1988; Haltenorth and Diller, 1980). Skins have been used to make karosses and fine suede for gloves (Kingdon, 1982). For sport hunting, Sclater and Thomas (1896–1897:91) said: "These small Antelopes are very easily knocked over with a shot-gun and No. 4 shot . . . The female exposes herself most, and is consequently most often shot." Dik-diks are reported to have a disagreeable, musky taste, and some hunters dislike them because they flush and warn larger game (Anonymous, 1957; Nowak, 1991).

On moonless nights, Guenther's dik-diks can be easily captured by hand after being blinded by a strong light (Ono et al., 1988). A technique for capturing and restraining captive animals by hand is described by Luce (1987). Home ranges determined by radiotelemetry were larger than territories estimated by the distribution of dung piles and preorbital gland deposits; weight of the radio transmitter, collar, and harness was 51.7 g, less than 2% of the body weight of the focal animals (Ono et al., 1988). *M. guentheri* dung piles can be distinguished from those of gray duikers (*Sylvicapra grimmia*) by their larger size and relatively smaller pellets, 6–8 mm in length; the grain-like pellets of male dik-diks are more pointed than those of females (Kingdon, 1982; Ono et al., 1988; Schoen, 1972). Husbandry and management of Guenther's dik-diks in captivity are described by Hnida et al. (1992).

**BEHAVIOR.** Guenther's dik-diks usually occur in groups of three to four, typically an adult pair with one or two immature offspring (Bryden, 1899; Estes, 1991; Roosevelt and Heller, 1915). Occasionally, pairs are in the company of others, and groups of six to 12 may be within sight of one another (Kingdon, 1982; Sclater and Thomas, 1896–1897). Members of a pair do not always stay together; they are often seen singly, but they stay closer together when moving outside their territory, and the male joins the female when the calf is born (Drake-Brockman, 1930; Kingdon, 1982; Kurt, 1964; Ono et al., 1988). Although a fixed territory is generally occupied by a pair, more than one adult female may share the territory of a male in areas where dik-diks occur in high densities. If one of the pair dies or disappears, a replacement may fill the territory almost immediately; on the other hand, the survivor may remain alone for several months (Drake-Brockman, 1930; Kingdon, 1982; Spinage, 1986).

As with most neotragines, dik-diks are monogamous (Estes, 1991). Estrous females increase their locomotor activity (i.e., walking) and social contact but decrease maintenance behavior, such as feeding and self-grooming; estrous females are constantly attended by their mates (Fitzgerald and Hnida, 1994b; Kingdon, 1982). The most obvious behavioral indicator of estrus is standing with a decurved flexing of the spine (lordosis). Although a female exhibits lordosis during courtship and copulation, an estrous female may present this posture when any conspecifics are present. Other indicators of estrus in Guenther's dik-diks include: anogenital grooming, anogenital sniffing of other individuals, and piloerecting the head crest and rubbing it against vegetation or other dik-diks (Hnida and Fitzgerald, 1992). In captivity, estrous females may approach their keeper and vocalize (Fitzgerald and Hnida, 1994b). During courtship, the female appears dazed, her movements slow down, and she keeps her nose raised while walking near the male. She may flag a ruff of white hair on each haunch while slowly flicking her tail; this seems to signal her receptivity to the male (Kingdon, 1982). Courtship behavior of the male includes: chasing; lowstretch approach and close following of the female; and sniffing and/or licking the female's preorbital gland, nose, and genitals. Receptive females respond to genital licking by raising their tail and squatting slightly; males then mount bipedally with their neck forward and forelegs folded, without clasping or resting on the female (Estes, 1991; Kingdon, 1982). Genital licking may be followed by urine testing, in which the male briefly lifts and wrinkles his proboscis to assess the hormonally the receptivity of his mate; however,

this behavior seems less important in dik-diks than in other antelopes. Kingdon (1982) postulates that the significance of urine testing in determining the female's receptivity may have been replaced by rump flagging and tail flicking in response to a need for water economy. A disturbance that brings a male and estrous female together can cause a rapid switch from alarm to sexual behavior (Kingdon, 1982).

Female *M. guentheri* stay with their young for the first day after parturition, taking frequent but brief absences to feed (Kingdon, 1982). After the first day, dams visit their calves about sunrise, midday, dusk, and midnight for ca. 15 min/visit; calves are suckled for 1–2 min, groomed, and after a short frolic, are returned to their hiding place or led to a new one by the dams. Sires also groom the young, and they will stop feeding in order to join their calves; juveniles often choose to rest beside their fathers (Kingdon, 1982). Males are watchful for predators while their mates feed, and it is possible, though unproven, that neotragine males actively intervene in response to distress bleating of their calves (Estes, 1991). Juveniles engage in mock fights; later, fathers begin to harass their male offspring. This may be related to the appearance of horns; thus, male offspring are forced to emigrate earlier than females (Estes, 1991; Kingdon, 1982). Among neotragines, young are driven out at an early age (i.e., before sexual maturity); since these species do not form bachelor groups, ousted youngsters must quickly learn to live independently (Spinage, 1986).

Guenther's dik-diks are predominantly diurnal, being most active from dawn until mid-morning and from mid-afternoon until after dark; they may remain active during a full moon (Kingdon, 1982; Ono et al., 1988). As concentrate selectors, dik-diks generally feed throughout the day, but their most intensive feeding occurs during midday. During the early afternoon heat, they stand or lie in the shade and groom, ruminate, or sleep (Estes, 1991; Hofmann, 1973, 1989). Dik-diks usually rest near a tree trunk, termitary, or thicket clump; at times, they sleep with the head flat on the ground and the eyes closed, making them difficult to see (Kingdon, 1982). From late afternoon until evening, they feed constantly while moving slowly about; mating and play generally occur during this time (Fraser, 1968; Hofmann, 1973). Guenther's dik-diks are believed to remain in their territories during the day, but they may forage far beyond their territorial boundaries at night (Ono et al., 1988). Hofmann (1973) indicates that the daily activity of Guenther's dik-dik resembles that of Kirk's dik-dik, which is recorded in detail by Hendrichs and Hendrichs (1971).

Guenther's dik-diks rarely feed intensively on one plant; instead, they wander about selecting a variety of vegetation. With their elongated proboscis, narrow muzzle and tongue, and small body size, they can select small leaves among thorns and obtain adequate nutrition within areas too small and sparse to support larger browsers (Estes, 1991; Hofmann, 1973). Guenther's dik-diks often use a foreleg to pull browse within reach, or they may rise into a bipedal position, supporting their forelegs on twigs, in order to reach food at higher levels. Succulent leaves are bitten off singly and slowly chewed (Hofmann, 1973). Dik-diks sometimes dig for roots and tubers with their hooves or horns (East, 1988; Kingdon, 1982; Roosevelt and Heller, 1915). Thomas (1894) suggests the proboscis may be used to search for bulbs in the soil.

Dik-dik vocalizations have been described as: a ringing "zik-zik," bird-like chirp, or whistling hiss made when alarmed or excited (Haltenorth and Diller, 1980; Roosevelt and Heller, 1915; Sclater and Thomas, 1896–1897); a squealing bleat made when caught or by calves when frightened (Kingdon, 1982); squeaks or twitters that are soft or inaudible to the human ear, made by females during estrus or to contact their hidden young (Estes, 1991; Fitzgerald and Hnida, 1994b; Kingdon, 1982); and an occasional grunt (Bryden, 1899). Whistles are accompanied by a sharp downward extension of the proboscis. Alarm whistling is most frequently and persistently done by males, perhaps functioning to define the territory or to maintain pair and family bonds by encouraging individuals to clump together; young are silent during the day, but they may whistle at night (Estes, 1991; Kingdon, 1982). When suddenly disturbed, dik-diks may dart away or bound (stot) in a circular direction and then turn around and stand with head erect to determine the source of disturbance; threat or excitement may also cause them to erect their crest or rump hairs (Kingdon, 1982; Sclater and Thomas, 1896–1897; Spinage, 1986; Walther, 1984).

Development of scent glands and scent-marking behavior suggests that olfactory communication is important to dik-diks, and

scents derived from pedal and preorbital gland secretions are likely used for marking territories (Estes, 1991; Leuthold, 1977). Guenther's dik-diks urinate and defecate on localized and repeatedly used dung piles that are up to 5 m² in size; distribution of these dung piles is related to territorial boundaries (Kingdon, 1982; Ono et al., 1988; Roosevelt and Heller, 1915). Establishment of dung sites may be one of the first acts in asserting a territory. This behavior may be learned: a mother leads her calf to the site where she defecates and then induces her young to do the same by licking the genital region. Males usually follow close behind females, smelling and testing their urine, and then urinating on the same spot (Kingdon, 1982). Before defecating, male dik-diks often paw the ground with one or both forefeet, presumably to add pedal gland scent to that of urine and dung, and forming a scrape that can be seen at a distance (Gosling, 1985; Leuthold, 1977; Walther, 1984). Dik-diks defecate over the dung of elephants, black rhinoceroses (*Diceros bicornis*), and antelopes; viverrids sometimes defecate on dik-dik latrines (Kingdon, 1982). Compared to dung piles, preorbital gland deposits are often more centrally located within the territory; thus, they may function primarily for self-orientation of the territory owner and secondarily for advertising the territory and deterring conspecific intruders (Ono et al., 1988). Females ordinarily use their preorbital glands less frequently than males, and placements of preorbital gland secretions by females on the horns of males are believed to express submission (Kingdon, 1982).

*Madoqua guentheri* territories often are demarcated by natural features such as drainages and paths, and they often consist of open ground with regularly spaced clumps of bush (Kingdon, 1982). Home ranges may correspond to territories of individual Guenther's dik-diks; in other instances, however, home ranges do not correspond directly to territories, and ranges of males may overlap by up to 65%. Home ranges of individuals in Omo National Park, Ethiopia varied from 4–6 ha to 8.5–13.7 ha in size; larger home ranges occurred during dry periods when Guenther's dik-diks moved into grassland (Ono et al., 1988). Distances (in m) between pairs were 200, 500, and 500–600 in Kenya (South Turkana), Uganda (Nabilatuk), and Ethiopia (Erer Valley), respectively (Coe, 1972; Kingdon, 1982; Kurt, 1964). On a daily basis, Guenther's dik-diks range over an average of 23–70% of their total home range, and most of the area within the home range is covered in 10–15 days (Ono et al., 1988). Individuals sometimes move independently of their mates for several days, and during these times, their ranges only partially overlap. Pairs occasionally shift their territories to neighboring regions, indicating that pair bonds in Guenther's dik-diks are independent of territorial bonds (Ono et al., 1988).

Dik-dik territories, including those of *M. guentheri*, are defended by males, and territorial behavior peaks when females are in estrus. Aggression between territorial males may involve dominance or threat displays (erect or head-up posture, high-stepping, object-homing, medial-horn presentation, and horn jabbing) and fighting (chasing, air-cushion fighting, horn-contact, and horn stabbing; Estes, 1991; Kingdon, 1982; Ono et al., 1988). Aggression is most common toward intruders into territories and between fathers and their adolescent sons. Submissive behavior includes head-low/chin-out posture, udder-seeking, and lying-out (Estes, 1991). Serious fighting is unusual, but horns are occasionally broken in fights; generally, dik-diks go through the motions of head butting while maintaining an air cushion between them (Estes, 1991; Kingdon, 1982).

The running gait of Guenther's dik-diks has been likened to that of civets (*Civettictis civetta*) and mongooses (*Herpestes* sp.; Roosevelt and Heller, 1915). They generally seek cover at the least alarm; frightened dik-diks race to the nearest vegetation and dive with their head down and wedge-shaped body forward (Hofmann, 1973; Kingdon, 1982). Sudden scares or warning cries of other animals elicit crouching and freezing, particularly when hyenas, lions, or humans are present. For the first week or so after parturition, dik-dik parents may startle their calves and cause this reaction; in which case, they come and nudge the youngsters into activity (Kingdon, 1982). Other forms of antipredator behavior include: standing watch while in alert posture, whistling snorts, stotting, sudden flight and dodging run, and distress bleating (Estes, 1991). They discriminate between predators and have different responses to hyenas and leopards: dik-diks whistle at leopards and watch them from a safe distance, but hyenas do not elicit whistling. Dik-diks have well developed hearing, sight, smell, and speed;
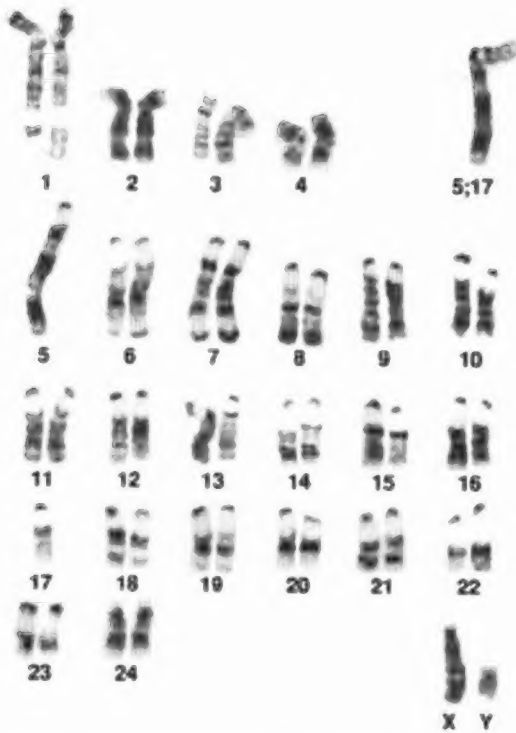
FIG. 4. G-banded karyotype (2n = 49) of a male *Madoqua guentheri* (studbook number 127; see Kumamoto, 1995), heterozygous for a Robertsonian translocation involving chromosomal pairs 5 and 17.

however, their best defense is probably knowing the home territory very well (Haltenorth and Diller, 1980; Kingdon, 1982). Leuthold (1977) postulated that dik-dik horns are shorter than the ideal needed for defense against predators (i.e., straight, pointed horns of medium length); females lack horns, further suggesting that they do not function as an antipredator weapon, but rather in social competition between males.

Guenther's dik-diks belong to a group of mammals, including species of artiodactyls, elephant shrews, lagomorphs, and rodents, which are behaviorally, ecologically, and morphologically convergent. These species exhibit what has been referred to as the "microcursorial adaptive syndrome" (Rathbun, 1979:64). Criteria that characterize this syndrome include: tropical and subtropical distribution; body size <20 kg; swift, cursorial locomotion; high energy, browse diet; precocial young; and monogamous social structure. Guenther's dik-diks have further similarities with other small species of antelopes: bush or forest habitat; small, stable home range and social group; year-round territory that generally coincides with home range; and antipredator behavior that relies on inconspicuousness (Leuthold, 1977). The dispersed nature of browse restricts food intake within the time available for feeding so small-sized browsers should have relatively low requirements for food quantity. On the other hand, browse production throughout the year allows an animal with low quantitative requirements to find sufficient food year-round within a relatively small area. Because competition can interfere with individual energy requirements, browse is more economically exploited by smaller groups. Low, thicket habitats lend themselves to the small body size, browse diet, and monogamous nature of *M. guentheri*. In keeping with their antipredator strategy of inconspicuousness, Guenther's dik-diks rely primarily on olfactory marking rather than visual or auditory displays to advertise territorial ownership (Leuthold, 1977).

**GENETICS.** Guenther's dik-diks have 2n = 48–50 chromosomes; 8–10 submetacentrics and 36–40 acrocentrics, with acrocentric sex chromosomes (Benirschke and Kumamoto, 1987; Fig. 4). Variation in diploid number is the result of a putative centric fusion, occurring in homozygous (2n = 48) and heterozygous (2n = 49) forms; individuals lacking the fusion are 2n = 50. Guenther's dik-diks captured near Lake Baringo, Kenya were either 2n = 48

or 2n = 50 (Kumamoto, 1995). Acrocentric autosomes exhibit pericentromeric heterochromatin; metacentrics are generally C-band negative, but those formed by the centric fusion have duplicate blocks of pericentromeric heterochromatin. A few autosomes are polymorphic in size due to terminal C-bands. The X has pericentromeric heterochromatin and a faint interstitial C-band, and the Y appears entirely heterochromatic (Benirschke and Kumamoto, 1987).

Mating between a 2n = 48 female and a 2n = 50 male resulted in heterozygous offspring. Male and female heterozygotes are chromosomally balanced and have reproduced successfully in captivity (Kumamoto, 1995). Hybridization between a *M. guentheri* male (2n = 50) and a *M. kirkii* female (2n = 46) resulted in offspring having 2n = 48. Male offspring were sterile; testes were reduced in size, whereas complete meiotic arrest and the absence of spermatozoa were indicated by histological and semen analyses (Ryder et al., 1989). Backcrossing an F1 hybrid female with a *M. guentheri* male produced a stillborn F2 (Kumamoto, 1995). Skins and skulls displaying intermediate or mixed characteristics of *M. guentheri* and *M. kirkii* have been found in Somalia (Webbe Shibeli drainage), Ethiopia (southern Galla), Kenya (South Turkana), and at the Kenya-Uganda border, suggesting that hybridization in natural populations is rare but occurs over a large area (Ansell, 1971; Kingdon, 1982; Poggesi et al., 1982).

In a captive population of Guenther's dik-diks, there was no allozymic variation detected in 22 protein-coded loci. However, abundant variation was demonstrated with DNA fingerprinting and randomly amplified polymorphic DNA (RAPD); mean band sharing was 46% and 63% for the DNA fingerprinting and RAPD analysis, respectively (S. K. Davis, in litt.).

**REMARKS.** Neotragines appear as conservative survivors from an early phase of bovid evolution. The Neotragini as a whole are not monophyletic, and *Madoqua* appears to be a sister taxon to species in the Antilopini (Gentry, 1992; Georgiadis et al., 1990). Dik-diks may have originally inhabited evergreen thickets at the base of the Ethiopian Highlands, a habitat now occupied by *M. saltiana*. In more open bush to the south, *M. guentheri* and *M. kirkii* are probably exposed to more heat and desiccation, and their more elongated snouts are thought to represent a later and more specialized adaptation for evaporative cooling (Estes, 1991). Evolution of *M. guentheri* and *M. kirkii* may be the result of climatic changes during Pleistocene; habitat suitable to dik-diks would have been opened during dry periods and closed during wet periods, resulting in alternating connection and isolation of populations (Kingdon, 1982). One hypothesis suggests that *M. guentheri* and *M. kirkii* diverged while isolated from each other in eastern and southwestern Africa, respectively, and *M. guentheri* continued to evolve a more efficient nasal cooler (i.e., longer nose) in the hot Turkana basin (Kingdon, 1982). When the less specialized, but ecologically more versatile, *M. kirkii* was re-connected with East Africa, it may have competed with and extensively replaced *M. guentheri*. Another hypothesis holds that *M. guentheri* and *M. kirkii* differentiated within East Africa while separated by a forest belt (Kingdon, 1982).

"Dik-dik" is an Arabic name derived from the "zik-zik" sound it makes when startled (Sclater and Thomas, 1896–1897). Other names for dik-diks include: *ainshu* (Abyssinian); *beni-israel*, *om-dig-dig* (Arabic), *shigaro* (Dorobo), *adallo* (Galla), *esiro* (Karamojong), *chizimba* (Kigogo), *kabii* (Kikamba), *wisi* (Kiliangulu), *nguyhuya* (Kinyaturu, Kisandawe), *tibi* (Kipokomo), *kizimba* (Kisagara), *erongo* (Kisamburu), *sala* (Kisukuma), *digidigi* or *dikidiki*, *suguya* (Kiswahili), *empanas*, *eng-omani* (Masai), *erongo* (Samburu), *seran* (Sebei), *gussulei*, *sagaro* or *sakaro* (Somali), *paa* (Swahili), *esoro*, *ethuro* (Turkana; Bryden, 1899; Drake-Brockman, 1930; Hofmann, 1973; Kingdon, 1982). Common names for the Guenther's dik-dik are large-snouted dikdik, le dik-dik de Guenther (French), Güntherdikdik (German), *sagari* (Rendile), *sakaro gussuli* or *ghussleh* (Somali; Bryden, 1899; Drake-Brockman, 1910; Haltenorth and Diller, 1980; Roosevelt and Heller, 1915). The Somali name is derived from the "ghuss, ghuss, ghuss" sound it makes when surprised (Drake-Brockman, 1910). *Madoqua* is derived from the Amharic *medaqqwa*, the gray duiker (D. W. Yalden, in litt.). The etymology of *Rhynchotragus* is *rhynkhos* (Greek: snout) and *tragos* (Greek: he-goat; Gotch, 1979). *M. guentheri* is named for Albert Günther, Keeper of Zoology at the British Museum

(Natural History) from 1875 to 1895 and the describer of *M. kirkii* (D. W. Yalden, in litt.).

An old native fable explains why dik-diks leave their droppings in a single place. "Long, long ago, so the story goes, the king of the dik-diks was running along gaily in the bush not looking where he was going and without a care in the world, when he slipped and fell in a huge deposit of *ndofu* (elephant) dung. In his anger the king called a meeting of his subjects and they decided to try to trip up a ndofu for themselves. Ever since, the dik-diks have been working together to collect a pile big enough for a passing ndofu to slip upon" (Beard, 1965:103).

Dik-diks of the subgenus *Rhynchotragus* that occur in Uganda and Ethiopia are listed as *M. guentheri* (see Ansell, 1971; East, 1988; Yalden et al., 1984). Thus, we believe that dik-diks referred to as "*kirkii*" by Hutchison (1970a, 1970b), Kurt (1964), Morel and Rodhain (1972), and Schoen (1969, 1972) probably represent *M. guentheri* and, therefore, are included in this account. Much of the pertinent literature on dik-diks is generalized, without specific mention of the particular species being addressed; however, we have included some of this general information in order to present a more complete picture of the biology of *M. guentheri*. We thank Kurt Benirschke, Peter Hoppe, Scott Davis, Jason Douglas, Rod East, Richard Estes, Lisa Fitzgerald, Peter Grubb, John Hnida, Marlys Houck, Ken Kelley, Karl Kranz, Alberto Simonetta, and Derek Yalden for the information, comments, and effort they shared.

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